CHARACTERIZATION AND RELATIONSHIPS OF THE SUBGENERA OF *ISONYCHIA* (EPHEMEROPTERA: OLIGONEURIIDAE)[1,2]

W.P. McCafferty[3]

ABSTRACT: Abdominal gill spination is shown to be of limited taxonomic value in North American *Isonychia:* Apical spines vary on gills 1-6 in larvae of the *bicolor* species group of the subgenus *Isonychia,* and apical spines vary on gill 7 of *Isonychia (Prionodes) sayi.* Subgeneric classification is justifiable; however, certain larvae are not separable to subgenus or species. A plesiomorphic phylogenetic position of *I. sayi* within the subgenus *Prionodes* is suggested since it shares some but not all synapomorphies with other *Prionodes.* Two alternative species phylogenies are presented and show *Isonychia* s.s. as either a monophyletic or paraphyletic group depending on the relationships of the *bicolor* group. A new subgenus *Borisonychia* is established for *Isonychia diversa* and is consistent with cladistics showing *I. diversa* to be intermediate between *Isonychia* s.s. and its more apomorphic sister lineage *Prionodes.* Male genitalia are clearly diagnostic of the subgenera. A synopsis of subgeneric and species group classification of the 18 North American species is given.

Isonychia is a well known genus of brushlegged mayflies that was recently revised for North and Central America by Kondratieff and Voshell (1984). Adults were delineated at the subgeneric and specific level in the work, but as the authors admitted, the larvae of certain species remain difficult, if not impossible, to distinguish. My research indicates that distinguishing larvae to subgenera is also problematic.

Examination of the gills of middle to late instar larvae has revealed inconsistencies in subgeneric abdominal gill characterization in the *bicolor* species group of the subgenus *Isonychia* and *I. sayi* of the subgenus *Prionodes.* It is important to recognize potential problems that key users may encounter because *Isonychia* larvae are among the most commonly sampled riffle-dwelling mayflies, especially in central and eastern North America. Ecologists and others often need to identify middle instar and older individuals for meaningful biological assessments. In addition, the method for keying larvae to species is now predicated on their subgeneric placement (see keys of Kondratieff and Voshell 1984).

Isonychia was divided into the subgenera *Isonychia* s.s. and *Prionodes* by Kondratieff and Voshell (1983). Structural characteristics of male adult styliger, female adult subanal plate, and shape of the eggs are distinct for these subgenera, and warrant the division. The condition of the larval forecoxal gills distinguishes these subgenera except for one species.

[1]Received June 6, 1988. Accepted July 11, 1988.

[2]Purdue University Experiment Station No. 11691.

[3]Department of Entomology, Purdue University, West Lafayette, IN 47907.

Also, adult penes can be clearly divided into two subgeneric types except for one other species. Explanations for these exceptions within the context of cladistics and the establishment of a new subgenus are taken up later under the subject of relationships.

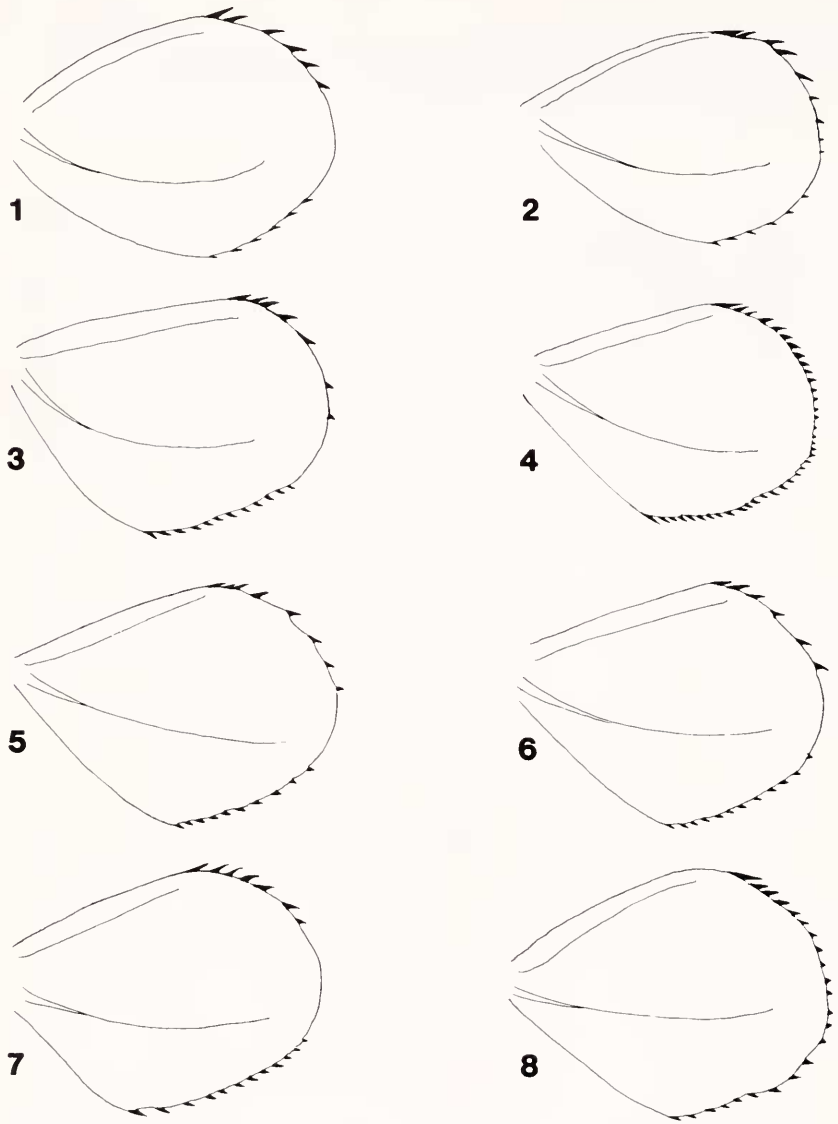
KEY CHARACTERISTICS

In the larval key of Kondratieff and Voshell (1983) *Prionodes* was said to have "posterior gills without apical stout spines" and "forecoxae gills single (except *I. sayi);*" whereas *Isonychia* s.s. was said to have "posterior gills with apical stout marginal spines" and "forecoxae gills in tufts." Under the description of *Isonychia* s.s., however, it was said that spines were on the apical margin "of all gills." Kondratieff and Voshell (1984) maintained use of these traits, with the exception that in their descriptions and key the apical spine character was applied to "abdominal gill lamella," with no specification of exact gills involved. Although abdominal gill 7 was the one illustrated in both of these studies, it must be presumed that the statements referred to all abdominal gills.

My study of the *bicolor* group indicates that abdominal gill spination varies among gills. I have examined *I. bicolor, I. rufa,* and *I. velma* of this group. Gills 1-5, and sometimes 1-6, of these species often lack apical spines (Fig. 1). Ultimate or penultimate instars tend to have apical spines on gills 4-7 (Figs. 3 and 4), but not always. There is also individual and population variation in the number of apical spines and the exact number of gills involved, with the more anterior gills more apt to lack apical spines. The character is further confounded by inevitable differences in interpretation of the actual limits of the apical margin of a rounded gill lamella. Gill 7 does appear always to have apical spines, but these can be weak (Fig. 2), and high magnification and special lighting are sometimes necessary to detect them because of the short, thick setae also situated along the margin. Unfortunately, gill 7 is easily broken off when specimens are collected or handled.

The often distinctively patterned larvae of *I. sicca* (see Provonsha and McCafferty 1982) of the *sicca* species group of *Isonychia* s.s. have apical spines on at least gills 3-7. There is no problem in placing them, and perhaps other *Isonychia* s.s. not treated here, to subgenus.

Larva of *I. sayi,* the only *Prionodes* species that could be confused with *Isonychia* s.s. because of its forecoxal gills, may or may not possess apical spines on abdominal gill 7, even within the same population and age class (Figs. 6 and 8). No other gills, however, possess apical spines (Figs. 5 and 7). Thus, certain individuals can be structurally similar to some of the *bicolor* group, and even the use of gill 7 is not failsafe.

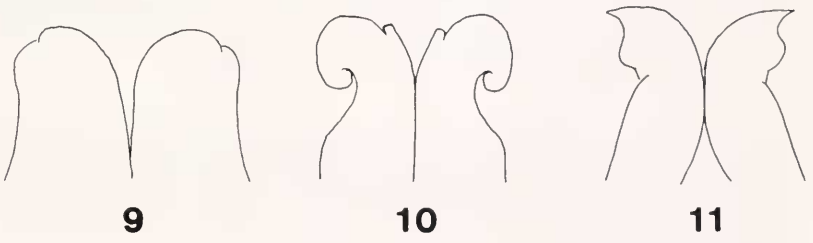


Figures 1-8. *Isonychia* larval abdominal gill lamellae. 1-2. *I. velma* (middle instar, California). 1. gill 6. 2, gill 7. 3-4. *I. bicolor* (last instar, Indiana). 3, gill 4. 4, gill 7. 5-6. *I. sayi* (typical middle instar, Florida). 5, gill 6. 6, gill 7. 7-8. *I. sayi* (atypical middle instar, Florida). 7, gill 6. 8, gill 7.

Using the simple forecoxal gill, larvae of the southeastern species *I. hoffmani, I. georgiae, I. notata,* and *I. obscura* key easly to *Prionodes* and can then be keyed to species. All known *Isonychia* s.s. larvae can be keyed by their multibranched forecoxal gills, but *I. sayi* would also key here. Furthermore, although the keys of Kondratieff and Voshell (1984) were an important advance, once the forecoxal gill type is determined, certain of these larvae may be impossible to key to species using present structural characters. For example, it is still doubtful if midwestern cohabiting *I. rufa* and *I. bicolor* can be differentiated by number of metafemoral cleft spines (couplet 5), and gill spination characters in couplet 2 only work "usually" and are very difficult to interpret (references to "gills 6-8" are obvious typographical errors). Use of color patterns of large series along with distributional data should lead to accurate identification of several species. These data can be gleaned from the comprehensive species treatments of Kondratieff and Voshell (1984), which are superior to those previously available from Traver (1935).

RELATIONSHIPS

Regarding cladistic relationships, *Prionodes* appears to be the most specialized subgenus as is illustrated by the apomorphic penes (Fig. 11) of that group as compared to those of *Isonychia* s.s. (Fig. 9). *Prionodes* penes have uniquely toothed, dorsally recurved, lateral lobes (see figures of Kondratieff and Voshell 1984). The reduction of the forecoxal gill to a single filament in *Prionodes* is also apomorphic. From this, it can be deduced that *I. sayi* is an early branched lineage within *Prionodes* (Figs. 12 and 13) because it does not share this apomorphic forecoxal gill, or an apomorphic two-spot marginal pigmentation of gill lamellae, with the other *Prionodes.* (I recognize these other *Prionodes* species as the *georgiae* species group.) This phylogenetic position may explain the tendency for



Figures 9-11. Outline shapes of *Isonychia* penes. 9, *I. (Isonychia) sicca.* 10, *I. (Borisonychia)* diversa. 11, *I. (Prionodes) obscura.*

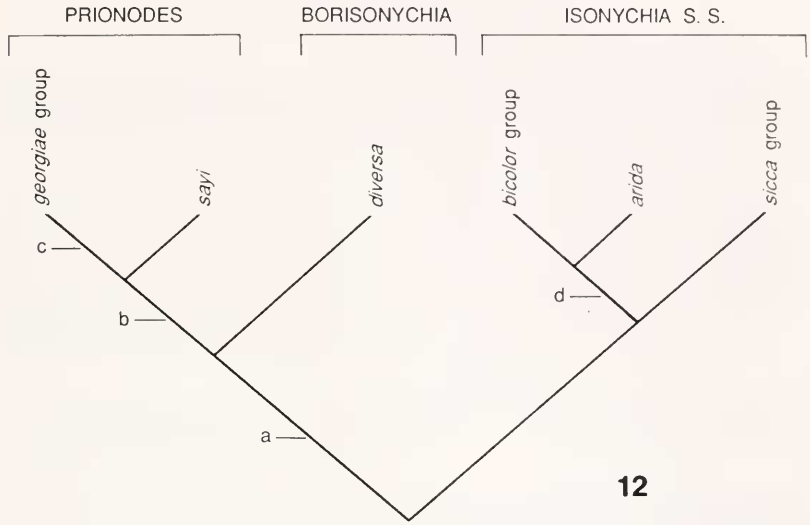
apical spines to remain on gill 7 in some individuals of *I. sayi,* since the characteristic is not totally lost, as it apparently is in the *georgiae* group lineage.

If the above hypotheses are correct it is possible that the *bicolor* group of *Isonychia* s.s. (a lineage that includes *I. arida*) shares an immediate common ancestor with *Prionodes* (Fig. 13). This possible relationship may be supported by the tendency in *bicolor* group species to lose apical gill spination in the anterior gills, sharing such a derivation with *Prionodes.* More cladistic data, however, are required before it can be resolved whether *Isonychia* s.s. is monophyletic (Fig. 12), or alternatively, paraphyletic (Fig. 13).

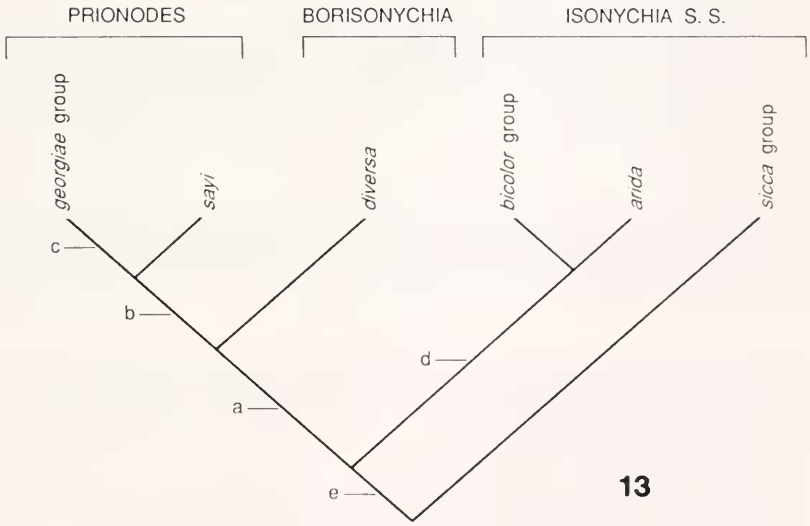
An important additional consideration in the phylogeny of *Isonychia* involves the position of *Isonychia diversa.* This species is known definitely only from the male adult holotype. It was placed in the subgenus *Isonychia* by Kondratieff and Voshell (1983), although they did not place it with any grouping of other species within *Isonychia* s.s. Whereas it retains a plesiomorphic styliger typical of *Isonychia* s.s., its penes (Fig. 10) are highly distinctive and appear intermediate between the plesiomorphic *Isonychia* s.s. (Fig. 9) and more apomorphic *Prionodes* (Fig. 11) penes types. The phyletic position of this species (Figs. 12 and 13) shows it to be a sister lineage to *Prionodes,* sharing initial lateral modifications of the penes. Regarding a female adult apparently taken with the holotype of *I. diversa,* Kondratieff and Voshell (1984) stated that, "this badly damaged specimen is similar to females of the *sicca* and *bicolor* groups." Even if this female is *I. diversa,* it is of no aid cladistically because of the plesiomorphic nature of the *sicca* and *bicolor* group females.

Isonychia diversa could be considered a primitive (early derived) member of *Prionodes,* and such a classification would be more consistent with its cladistic relationships than is the prior *Isonychia* s.s. classification. Moreover, the recognition of a separate subgenus for *I. diversa* is also consistent with its cladistics. Because its genitalia are highly distinctive, and because the male genitalia are definitive descriptors of the subgenera as established by Kondratieff and Voshell (1983), I am herewith establishing a new subgenus for *I. diversa.* I am pleased to name this taxon after the given name of Dr. Boris Kondratieff.

Figures 12 and 13. Hypothetical phyletic relationships of *Isonychia* species and species groups in North America. 12. First alternative cladogram showing monophyletic subgenus *Isonychia.* 13. Second alternative cladogram showing paraphyletic subgenus *Isonychia.* Indicated synapomorphies: a - penes latterally developed, b - penes with acute lateral processes, c - forecoxal gill single, d - penes with dorsal flap, e - tendency for loss of spination on anterior abdominal gills.


PRIONODES
BORISONYCHIA
ISONYCHIA S. S.
georgiae group
sayi
diversa
bicolor group
arida
sicca group
c
b
d
a

12


PRIONODES
BORISONYCHIA
ISONYCHIA S. S.
georgiae group
sayi
diversa
bicolor group
arida
sicca group
c
b
d
a
e

13

Borisonychia new subgenus

Type species: *Isonychia diversa* Traver, 1934:244.

Diagnosis: *Borisonychia* is distinguished from other *Isonychia* subgenera by the adult penes (Fig. 10) that..."are suddenly incurved and then curve outward again forming more or less rounded apical lobes, which are separated by a median V-shaped notch. Each lobe bears a slight indentation on its apical margin." (Traver 1934).

The classification of North American *Isonychia* can thus be summarized as follows:

Subgenus *Isonychia* s.s.
sicca species group: *I. berneri* Kondratieff and Voshell; *I. campestris* McDunnough; *I. edmundsi* Kondratieff and Voshell; *I. intermedia* (Eaton); *I. sicca* (Walsh).
arida species group: *I. arida* (Say).
bicolor species group: *I. bicolor* (Walker); *I. rufa* McDunnough; *I. tuscalensis* Berner; *I. velma* Needham.

Subgenus *Borisonychia* McCafferty
diversa species group: *I. diversa* Traver.

Subgenus *Prionodes* Kondratieff and Voshell
sayi species group: *I. sayi* Burks.
georgiae species group: *I. hoffmani* Kondratieff and Voshell; *I. georgiae* McDunnough; *I. notata* Traver; *I. obscura* Traver; *I. serrata* Traver; *I. similis* Traver.

ACKNOWLEDGMENTS

I am grateful to Michael Mischuk of Appleton, WI and Wills Flowers of Tallahassee, FL for providing extra specimens for examination, and to Dan Bloodgood and Arwin Provonsha of West Lafayette, IN for illustrations.

LITERATURE CITED

Kondratieff, B.C. and J.R. Voshell. 1983. Subgeneric and species-group classification of the mayfly genus *Isonychia* in North America (Ephemeroptera: Oligoneuriidae) Proc. Entomol. Soc. Wash. 85: 128-138.

_____. 1984. The North and Central American species of *Isonychia* (Ephemeroptera: Oligoneuriidae). Trans. Amer. Entomol. Soc. 110: 129-244.

Provonsha, A.V. and W.P. McCafferty. 1982. New species and previously undescribed larvae of North American Ephemeroptera. J. Kans. Entomol. Soc. 55: 23-33.

Traver, J.R. 1934. New North American species of mayflies (Ephemerida). J. Elisha Mitchell Sci. Soc. 50: 189-254.

_____. 1935. Part II, Systematic, pp. 239-739 *In* Needham, J.G., J.R. Traver, and Y-C. Hsu, The Biology of Mayflies. Comstock, Ithaca, N.Y.